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HOLOPLANKTONIC MOLLUSCS (GASTROPODA: PTEROTRACHEOIDEA, THECOSOMATA AND GYMNOSOMATA) FROM THE SOUTHERN MEXICAN PACIFIC

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ABSTRACT

This is the first study of species composition of holoplanktonic molluscs of the Pacific coast of southern Mexico, focusing mainly on the Gulf of Tehuantepec. From two oceanographic surveys during summer 2007 and 2010, 40 zooplankton samples were obtained. A total of 40 species contained within 17 genera and 8 families was found. The results show 15 range extensions, including *Atlanta californiensis* and *Carinaria japonica* which were previously considered as endemic to the Transition Zone waters of the California Current, and *Limacina helicina* which was thought to only inhabit polar and subpolar waters. *Atlanta gibbosa* and *Creseis chierchiae* f. *constricta* are two new records for the American Pacific. The use of holoplanktonic molluscs as indicators of water masses is a common practice; however, these reported range extensions limit the validity of their use as indicators, at least within the environmental parameters established in previous studies. Although the 40 species found represent only 43% of the species recorded for the Pacific Ocean, it is noted that this species richness only represents summer conditions and an increase could be expected if sampling was extended to winter.

INTRODUCTION

Holoplanktonic molluscs spend their entire life cycle in the water column. They are classified into two informal groups: (1) superfamily Pterotracheoidea (Heteropoda) in the Architaenioglossa and (2) the clades Thecosomata and Gymnosomata in the Opisthobranchia (commonly referred to as pteropods).

These organisms are abundant within the zooplankton and feed upon fish larvae, copepods, ctenophores and other molluscs; in turn, they are food for organisms such as fish, turtles and jellyfish (Ralph, 1957; Lalli & Gilmer, 1989). Due to their diel vertical migrations, they serve as vectors of energy transference through the water column (Lalli & Gilmer, 1989; Van der Spoel & Dadon, 1999; Castro & Huber, 2007). It has recently been observed that shelled holoplanktonic molluscs are of ecological interest, as they contribute significantly to the carbon cycle in the ocean (Lalli & Gilmer, 1989; Fabry, 1990) and it has been hypothesized that long-term variations in the distribution and abundance of these organisms may reflect the effect of global climate change in the oceans (Comeau *et al.*, 2009). Unfortunately, very little is known about the natural variations in the composition, distribution and abundance of holoplanktonic molluscs in the world's oceans. In view of the implications of the relationship between ecological changes and these animals, it is important to establish where and how holoplanktonic molluscs are distributed, in order to understand long-term variations and the implications of these changes.

There are about 40,000 known marine gastropods (Lalli & Gilmer, 1989), of which only 244 are considered holoplanktonic (Van der Spoel, Newman & Estep, 1997). In the Pacific Ocean, 34 species of heteropods and 69 species of pteropods have been recorded (Richter & Seapy, 1999; Van der Spoel & Dadon, 1999). For the Mexican Pacific, there are reports of 57 species from the Gulf of California and the Pacific coast of the Baja California Peninsula (Sánchez-Hidalgo y Anda, 1989; Angulo-Campillo, Aceves-Medina & Avendaño-Ibarra, 2011). There are also reports of 28 species from the Pacific coast of Costa Rica (Suárez-Morales, Gasca & Castellanos, 2009).

The Gulf of Tehuantepec, Mexico, is one of the most productive and diverse ecosystems within the Eastern Tropical Pacific Ocean. This is due to oceanographic and meteorological processes and the resulting ecological conditions in the area (Ortega-García *et al.*, 2000). To date, there has been a lack of systematic studies on the species composition of this important region. The present study records for the first time the species composition of holoplanktonic molluscs found in the Gulf of Tehuantepec, based on two summer oceanographic surveys.

MATERIAL AND METHODS

The Gulf of Tehuantepec is located in the southern Mexican Pacific. Its northern boundary (16°20′N) is the coastal line between Puerto Angel, Oaxaca (97°W) and Puerto Madero, Chiapas (92°W) and its southern limit is at 12°N latitude, covering a total area of 125,000 km^2. Two oceanographic surveys were conducted in the Gulf of Tehuantepec from 3 to 12 July, 2007 (TEHUANO 0707) and 14 to 27 June, 2010 (TEHUANO 0610) on board the oceanographic vessel ARM BI-03 *Altair* from the Secretaría de Marina-Armada de México (Fig. 1, Table 1).

Zooplankton samples were taken using oblique tows of bongo nets with flexible nytex collectors, following the sampling method described by Smith & Richardson (1979). A total of 16 samples was obtained from the 333 μm mesh net used during the 2007 survey, and 24 samples from the 505 μm mesh net used during the 2010 survey. These were analysed without fractionating to separate the holoplanktonic molluscs. The organisms were fixed and preserved in 96% ethanol to avoid shell deterioration. The sampling depth of the stations, as well as the coordinates and sampling times, are given in Table 1.

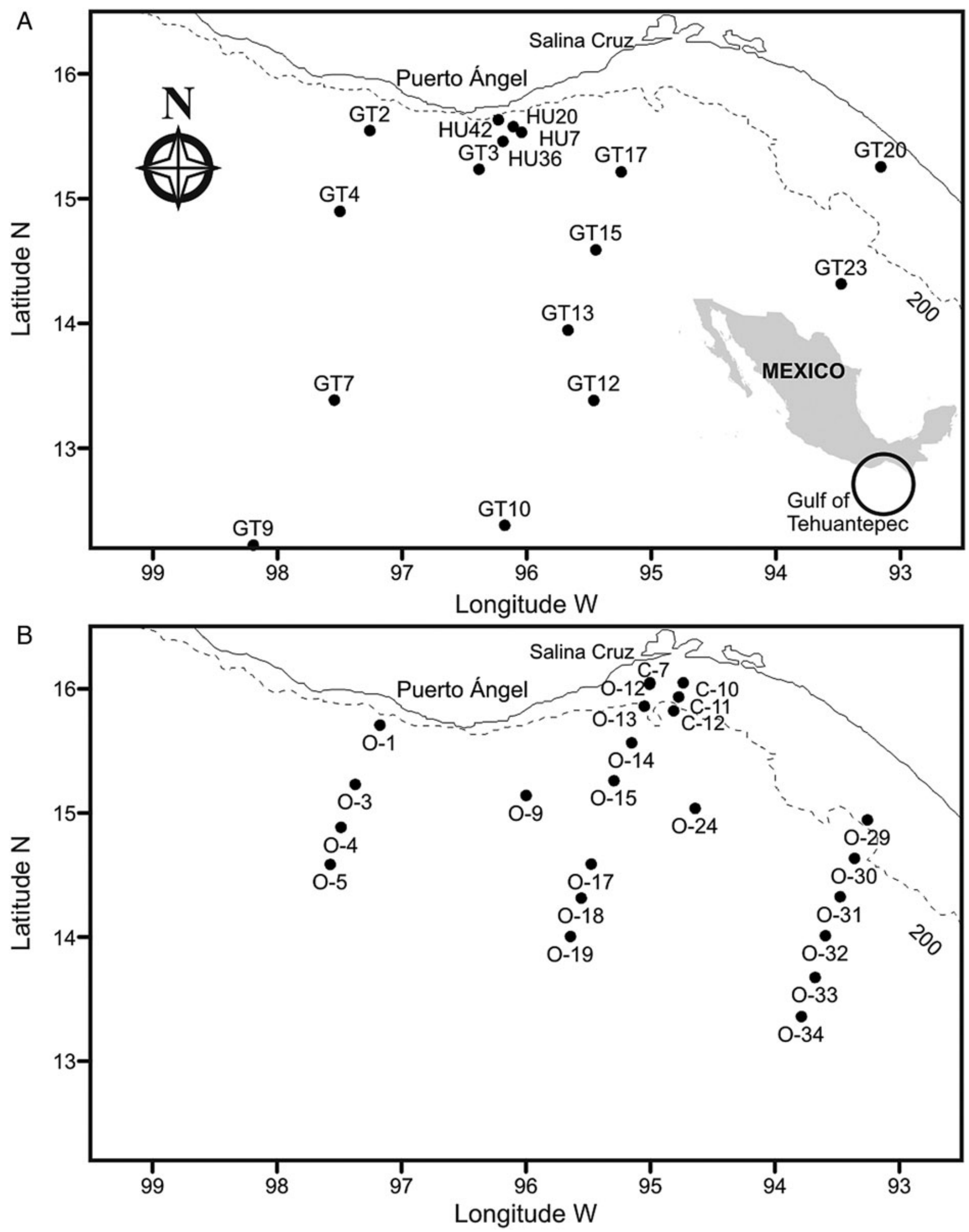

Figure 1. Study area and sampling stations. **A.** July 2007 (TEHUANO 0707). **B.** June 2010 (TEHUANO 0610). The dashed line indicates the 200 m isobath.

Table 1. Survey stations, time, date, sampling depth and coordinates for July 2007 (TEHUANO 0707) and June 2010 (TEHUANO 0610).

Station	Date	Hour	Depth (m)	Latitude (N)	Longitude (W)
TEHUANO 0707					
GT2	05/07/2007	23:43	179	15.54462	−97.25896
GT3	06/07/2007	03:16	214	15.23456	−96.38295
GT4	06/07/2007	07:11	214	14.89816	−97.49911
GT7	06/07/2007	21:25	214	13.38559	−97.54376
GT9	07/07/2007	11:05	214	12.22392	−98.19449
GT10	08/07/2007	06:48	214	12.38242	−96.17675
GT12	08/07/2007	20:05	214	13.38316	−95.46226
GT13	09/07/2007	12:25	179	13.94579	−95.66866
GT15	11/07/2007	18:49	179	14.58936	−95.44573
GT17	12/07/2007	03:15	214	15.2137	−95.24171
GT20	10/07/2007	23:42	21	15.25461	−93.15886
GT23	10/07/2007	13:20	179	14.31604	−93.47647
HU7	03/07/2007	22:33	179	15.53146	−96.04198
HU20	04/07/2007	06:25	179	15.57611	−96.10785
HU36	05/07/2007	09:26	214	15.45837	−96.19107
HU42	03/07/2007	13:53	143	15.63099	−96.2278
TEHUANO 0610					
O-12	14/06/2010	16:55	21	16. 0496	−95.00544
O-13	14/06/2010	22:28	150	15.86014	−95.04892
O-14	15/06/2010	03:07	179	15.56484	−95.15091
O-15	15/06/2010	08:29	186	15.25976	−95.29332
C-7	16/06/2010	13:30	21	16.03703	−95.00748
C-12	16/06/2010	21:13	143	15.8226	−94.81325
C-11	17/06/2010	00:18	71	15.9348	−94.77371
C-10	17/06/2010	02:16	29	16.0494	−94.73643
O-29	19/06/2010	01:33	43	14.94313	−93.25723
O-30	19/06/2010	05:53	179	14.63361	−93.36105
O-31	19/06/2010	10:39	214	14.32496	93.47599
O-32	19/06/2010	15:35	214	14.00997	−93.5945
O-33	19/06/2010	21:34	214	13.67373	−93.67753
O-34	20/06/2010	02:55	179	13.35885	−93.78768
O-24	21/06/2010	05:25	214	15.0365	−94.64107
O-9	25/06/2010	02:49	214	15.14146	−95.9993
O-17	25/06/2010	19:29	214	14.58778	−95.47577
O-18	26/06/2010	00:08	214	14.31316	−95.55614
O-19	26/06/2010	05:36	214	14.0042	−95.64288
O-5	27/06/2010	01:32	214	14.58456	−97.57187
O-4	27/06/2010	05:59	214	14.88435	−97.48555
O-3	27/06/2010	10:41	179	15.2293	−97.3718
O-1	27/06/2010	18:01	214	15.70778	−97.17368

After each tow at every sampling station, water temperature and salinity data were recorded using a conductivity/temperature/depth profiler (CTD) reaching to 600 m depth when the station depth allowed, or 10 m above the sea floor at shallower stations. To assess the water masses that were present in both studies, a temperature/salinity (T/S) diagram was constructed with the data obtained from the CTD.

The specimens were identified following the criteria established by McGowan (1960), Bé & Gilmer (1977), Richter & Seapy (1999) and Van der Spoel & Dadon (1999). The taxonomy in the species list follows Richter & Seapy (1999), Van der Spoel & Dadon (1999) and Janssen (2007, 2012), with family-level assignments according to Bouchet & Rocroi (2005).

An adjusted cumulative species curve was created in order to obtain an estimation of the total species richness of holoplanktonic molluscs in the Gulf of Tehuantepec. This was created using the EstimateS v. 9.1.0 software (Colwell, 2013), by generating an abundance matrix of species *vs* sampling station. This program takes data from a standardized sampling system, randomizes all the information and performs calculations on the number of observed and expected species using estimates and considering standard deviations from the scrambling process. The Chao diversity index was also calculated to estimate the number of species missing. The slope between each data point obtained with EstimateS was calculated to evaluate the approximation of the data to the function asymptote, at which the slope reaches zero. According to Jiménez-Valverde & Hortal (2003) the function asymptote predicts the total number of species that could be found.

RESULTS

A total of 21,447 organisms were obtained, 9,986 from the TEHUANO0707 survey and 11,461 from the TEHUANO 0610

Table 2. Species of holoplanktonic molluscs found in the Gulf of Tehuantepec during the July 2007 and June 2010 surveys.

Taxon	July 2007	June 2010	References
Informal group Architaenioglossa			
Clade Littorinimorpha			
Superfamily Pterotracheoidea (=Heteropoda)			
Familiy Atlantidae			
Atlanta brunnea Gray, 1850	X	X	1,2
Atlanta californiensis Seapy & Richter, 1993	X		2
Atlanta echinogyra Richter, 1972	X	X	2
Atlanta frontieri Richter, 1993	X		2
Atlanta gaudichaudi Souleyet, 1852	X	X	1, 2, 3
Atlanta gibbosa Souleyet, 1852	X	X	
Atlanta helicinoidea Gray, 1850	X	X	1, 2
Atlanta inclinata Gray, 1850	X	X	1, 2, 3
Atlanta lesueurii Gray, 1850	X	X	1, 2, 3
Atlanta oligogyra Tesch, 1806	X	X	2
Atlanta peronii Lesueur, 1817	X	X	1, 2, 3, 4
Atlanta plana Richter, 1972	X	X	2
Atlanta tokiokai Van der Spoel & Troost, 1972	X	X	1, 2
Atlanta turriculata d'Orbigny, 1836	X	X	1, 2, 3
Atlanta sp. 1	X	X	
Atlanta sp. 2	X		
Atlanta sp. 3	X		
Oxygyrus inflatus Benson, 1835	X	X	1, 2
Protatlanta souleyeti (Smith, 1888)		X	1, 2
Family Carinariidae			
Carinaria japonica Okutani, 1955	X	X	2, 3, 4
Carinaria spp.	X		
Cardiapoda placenta (Lesson, 1830)	X	X	1, 2, 3
Cardiapoda richardi Vayssière, 1904	X	X	1, 2, 3
Family Pterotracheidae			
Pterotrachea coronata Forskål, 1775		X	1, 2, 3, 4
Informal group Opisthobranchia			
Clade Thecosomata			
Superfamily Cavolinioidea (=Euthecosomata)			
Family Cavoliniidae			
Subfamily Cavoliniinae			
Diacavolinia longirostris (Blainville, 1821)	X	X	1, 2
Diacria quadridentata (Lesueur, 1821)	X	X	1, 2, 3, 4
Subfamily Clioninae Jeffreys, 1869			
Clio pyramidata lanceolata Lesueur, 1813	X	X	1, 2, 3, 4
Creseis clava (Rang, 1828)	X	X	1,2
Creseis chierchiae (Boas, 1886)	X	X	2
Creseis chierchiae f. *constricta* Chen & Bé, 1964		X	
Creseis conica Eschscholtz, 1829	X	X	1, 2
Creseis virgula Rang, 1928	X	X	3
Hyalocylis striata (Rang, 1828)	X	X	1, 2, 4
Familiy Limacinidae			
Limacina helicina (Phipps, 1774)	X	X	2, 3
Limacina inflata (d'Orbigny, 1836)	X	X	1, 2, 3, 4
Limacina trochiformis (d'Orbigny, 1836)	X	X	2, 3, 4
Clade Gymnosomata			
Superfamily Clionoidea			
Family Clionidae			
Subfamily Clioninae			
Clione limacina (Phipps, 1774)	X	X	2, 4
Subfamily Thliptodontinae			
Thliptodon diaphanus (Meisenheimer, 1903)	X		2
Family Cliopsidae			

Continued

Table 2. *Continued*

Taxon	July 2007	June 2010	References
Cliopsis krohni Troschel, 1854		X	2
Family Pneumodermatidae			
Pneumoderma atlanticum pacificum (Dall, 1815)	X	X	2
Pneumoderma spp.	X		
Pneumodermopsis ciliata (Gegenbaur, 1855)	X		2
Pneumodermopsis sp.	X		2

X denotes presence on each cruise. References indicate previous records for the American Pacific: (1) Suárez-Morales et al., (2009); (2) Angulo-Campillo et al., (2011); (3) McGowan, (1967); (4) Sánchez- Hidalgo y Anda (1989).

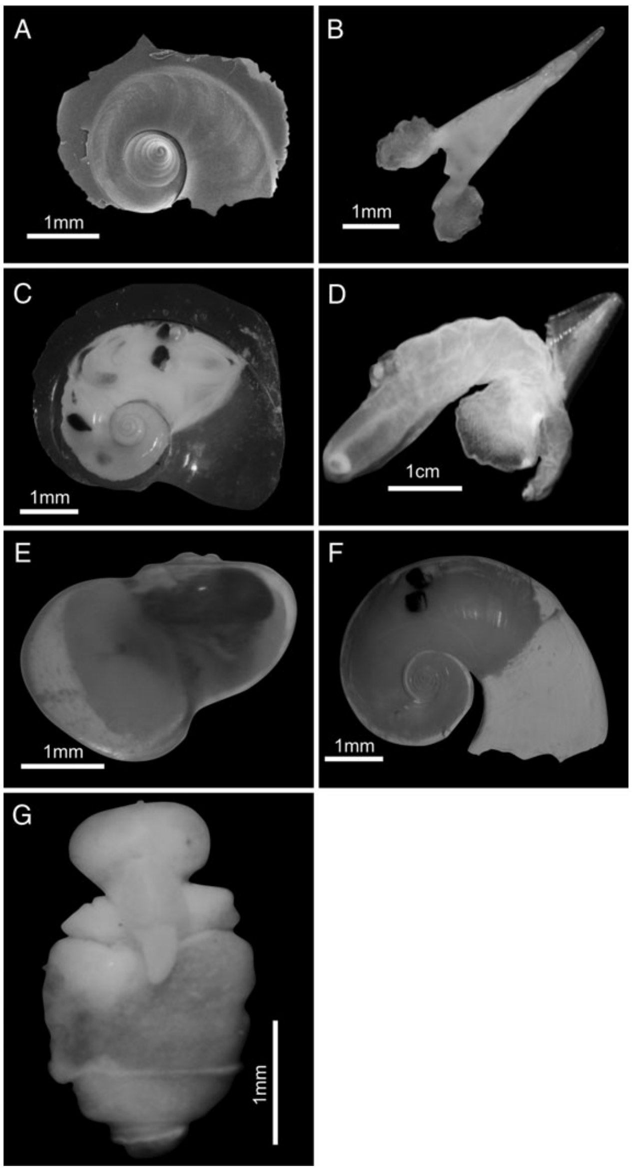

Figure 2. A. *Atlanta gibbosa*. **B.** *Creseis chierchiae* f. *constricta*. **C.** *Atlanta californiensis*. **D.** *Carinaria japonica*. E. *Limacina helicina*. **F.** *Atlanta* sp. 1. **G.** *Pneumodermopsis* sp. Scale bars: **A–C** = 1.0 mm; **D** = 1.0 cm; **E-G** = 1.0 mm.

survey. The organisms were identified as belonging to 40 species in 17 genera and 8 families. The Pterotracheoidea were represented by 24 species, the Thecosomata by 13 species and the Gymnosomata by 7 species (Table 2).

Two species were new records for the American Pacific: *Atlanta gibbosa* (Fig. 2A*)* and *Creseis chierchiae* f. *constricta* (Fig. 2B). Also, 15 range extensions were recorded, including *Atlanta californiensis* (Fig. 2C) and *Carinaria japonica* (Fig. 2D), both considered previously as indicators of the California Current, and *Limacina helicina* (Fig. 2E) considered as an indicator of polar water (Table 3).

The species that were only identified to genera, such as *Atlanta* sp. 1 (Fig. 2F) and *Pneumodermopsis* sp. (Fig. 2G), appear to represent undescribed species.

The cumulative species curve (Fig. 3) shows the number of species per sampling station that were found, with confidence intervals. It also shows that the inventory of species for the Gulf of Tehuantepec for summer has not reached the asymptote, as the minimum slope calculated was 0.17. The Chao diversity index calculates higher values of expected species per sampling station, likewise showing that the species inventory is not complete.

DISCUSSION

The 40 species of holoplanktonic molluscs found in the Gulf of Tehuantepec represent 58% of the total recorded from the American Pacific (Suárez-Morales *et al.*, 2009; Angulo-Campillo *et al.*, 2011). This total includes 86% of the Pterotracheoidea, 78% of the Gymnosomata and 41% of the Thecosomata of the American Pacific, confirming that the Gulf of Tehuantepec is an area of high diversity.

Although it is known that many holoplanktonic molluscs have a worldwide distribution, the pterotracheoideans are mainly distributed in warm waters, while thecosomes are found in temperate waters where they are of higher diversity (Lalli & Gilmer, 1989; Richter & Seapy, 1999; Van der Spoel & Dadon, 1999). Based on these contrasting affinities, the species composition in the Gulf of Tehuantepec reflects both the tropical affinities of the area and the summer season of the sampling period. Regarding the gymnosomes, Dadon & Chauvin (1998) and Van der Spoel & Dadon (1999) remarked that these are generally scarce, probably because of their highly specialized carnivorous habits, which makes them solitary organisms. Nevertheless, this group was well represented in terms of number of species.

Two new records for the American Pacific are the pterotracheoidean *Atlanta gibbosa*, which has only been reported from the Indo-Pacific (Seapy, 1990; Van der Spoel *et al.*, 1997; Richter & Seapy, 1999; Seapy, Lalli & Wells, 2003), and the thecosome *Creseis chierchiae* f. *constricta*, which has only been reported from

Table 3. New records of holoplanktonic molluscs for the American Pacific and range extensions.

Species	Known range				Ref.	Status
	Atlantic Ocean	Pacific Ocean	Indian Ocean	Pacific Ocean Distribution		
Atlanta californiensis	–	X	–	NP,CC,GC	1,5	RE
Atlanta echinogyra	–	X	X	GC	1,3	RE
Atlanta frontieri	X	X	X	GC	1,3	RE
Atlanta gibbosa	X?	X	X	IP	1,8	NR
Atlanta helicinoidea	X	X	X	GC,CR	1,3,7	RE
Atlanta oligogyra	X	X	X	GC	1,3	RE
Atlanta plana	–	X	X	GC	1,3	RE
Carinaria japonica	–	X	–	NP,CC,GC	1,3,4,6	RE
Clione limacina	X	X	X	CC,GC	2	RE
Cliopsis krohni	X	X	X	GC	2	RE
Creseis chierchiae	X	X	X	GC	2	RE
Creseis chierchiae f. *constricta*	X	X	X	IP	2	NR
Creseis virgula	X	X	X	CC,GC	2,3,4	RE
Limacina helicina	X	X	X	CC,GC	2,3,4	RE
Pneumoderma atlanticum pacificum	–	X	–	GC	3	RE
Pneumodermopsis ciliata	–	X	–	GC	3	RE
Pneumodermopsis sp.	–	X	–	GC	3	RE
Thliptodon diaphanus	–	X	–	GC	2,3	RE

NP, North Pacific; CC, California Current; GC, Gulf of California; IP, Indo-Pacific; CR, Costa Rica Pacific coast. References (Ref.): (1) Richter & Seapy (1999); (2) Van der Spoel & Dadon (1999); (3) Angulo-Campillo *et al.* (2011); (4) McGowan (1967); (5) Seapy & Richter (1993); (6) Seapy (1974); (7) Suárez-Morales *et al.* (2009); (8) Seapy, Lalli & Wells, (2003). Status indicated as: range extension (RE) or new record (NR) for the American Pacific.

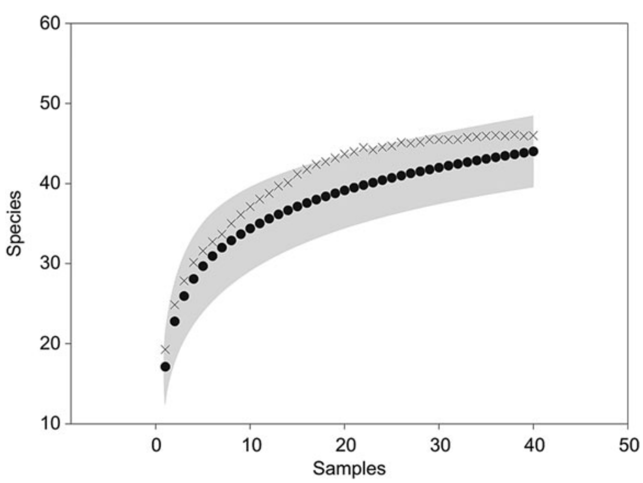

Figure 3. Adjusted cumulative species curve for the Gulf of Tehuantepec. Symbols: dots, calculated cumulative curve; crosses, calculated Chao index; grey area, confidence interval.

the North Atlantic (Bé & Gilmer, 1977; Van der Spoel *et al.*, 1997), the Gulf of Taiwan and the South China Sea (Rottman, 1976).

Among the new range extensions, it is worth noting the records of the pterotracheoideans *Atlanta californiensis* and *Carinaria japonica*, which have been considered to be restricted to the transition zone of the North Pacific faunistic province (Richter & Seapy, 1999), and the thecosome *Limacina helicina*, which has been considered an indicator of polar and subpolar water masses (McGowan, 1960; Bé & Gilmer, 1977). This is not the first time that this species have been observed beyond their typical distributional range. Angulo-Campillo *et al.* (2011) reported the presence of these three species in the Gulf of California and suggested that this may have been due to the intrusion of water from the California Current. However, this hypothesis can be rejected for the Gulf of Tehuantepec because, according to the T/S diagram for the sampling periods (Fig. 4), the area was dominated by tropical superficial and tropical subsuperficial waters, and there was no physical or chemical data that suggested the presence of water from the California Current or intrusion of Polar water masses at the surface. The water mass characterized by Fiedler & Tally (2006) as Antarctic Intermediate Water (AAIW) is present in the eastern tropical Pacific between 500 and 1000 m, and thus has no influence at the sampling depth of the present study. This suggests that the status of these three species as indicators of water masses should be reconsidered and their ranges should be extended southwards.

The cumulative species curve (Fig. 3) had not approached its asymptote, implying that the total number of species could increase with further sampling (Jiménez-Valverde & Hortal, 2003). This is also supported by the Chao index, which shows greater expected values of species for the area. These organisms are known to show seasonal variation (Fernández-Álamo, Sanvicente-Añorve & Alameda-de-la-Mora, 2000; Angulo-Campillo, 2009). For these reasons, if the sampling effort is increased, and especially if extended into the winter, it is probable that the number of species recorded for the area will increase.

This study emphasizes the need to document the real distributions of holoplanktonic species worldwide. Although some areas of the ocean have been thoroughly explored, such as the California Current, others remain poorly known. This probably explains the unexpected findings of *Limacina helicina*, *Carinaria japonica* and *Atlanta californiensis* in our sampling of this understudied region.

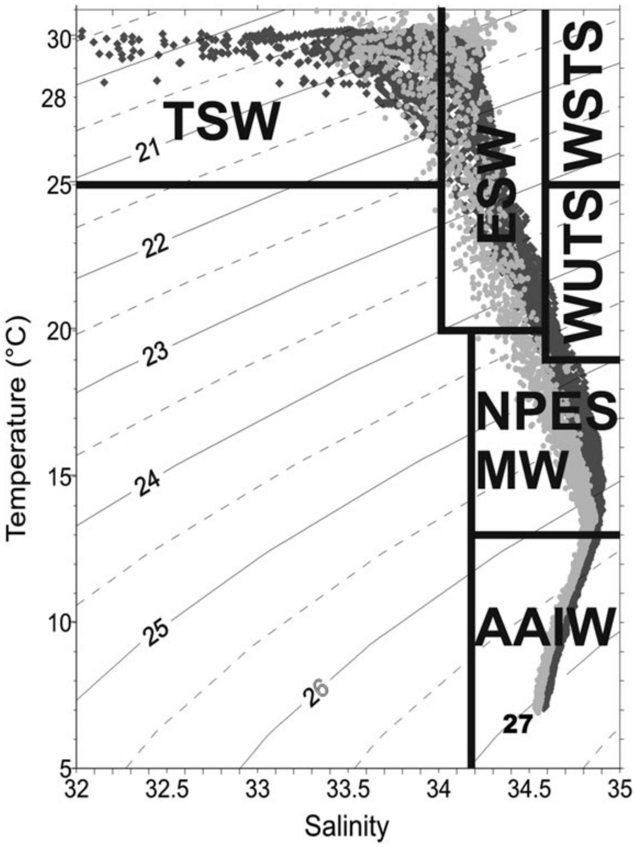

Figure 4. Water mass classification according to temperature and salinity (T/S) for both sampling periods: July 2007 (black dots) and June 2010 (grey rhombs). Abbreviations: TSW, Tropical Surface Water; ESW, Equatorial Surface Water; STSW, Subtropical surface Water; STUW, Subtropical Underwater; NPESMW, North Pacific Eastern Subtropical Mode Water; AAIW, Antarctic Intermediate Water.

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